

### 7.1 Introduction

This chapter is divided into two parts, each concerned with entities larger than populations. In the first part (section 7.2) we go beyond the traditional boundary of population ecology to consider the concept of a metapopulation, a set of local populations which interact via individuals moving among populations (Hanski & Gilpin, 1991). In Chapter 6, we examined the central issue of population ecology, namely population regulation. However, it is probable that some populations are not tightly regulated; they do not persist in one location for long periods of time at densities between positive limits. Sets of such populations may nevertheless persist in the same *region*, and therefore their regulation and long-term persistence also depends on extinction and colonization events of local populations rather than only with the birth and death processes (section 1.1) occurring *within* the local populations. We shall consider the elementary models of metapopulation dynamics, an example of a species with a metapopulation structure, and look at other areas of ecology to which the metapopulation concept is likely to have applications in the future.

The subject matter of this book is the ecology of populations, and it would be unreasonable, in the second part of this final chapter (section 7.3), to attempt to cover the ground of some other book concerned with the ecology of communities. Nevertheless, it will be valuable to consider, briefly, the roles that the various processes considered in the earlier chapters play in determining community structure. Specifically, we shall consider, in turn, the roles that interspecific competition, predation, disturbance, instability, and habitat size and diversity can play; and then draw what conclusions we can regarding their general importance in actual communities.

### 7.2 Metapopulation dynamics

The term metapopulation was coined by Levins (1970), though Andrewartha and Birch (1954) were among the first ecologists to acknowledge that models of single, isolated populations were inadequate for describing the dynamics of species in which local populations frequently become extinct.

The metapopulation concept has taken some time to develop and the reasons may be that ecologists were unclear that Levins had said anything new, and that the literature on colonization and extinction at the time was dominated by MacArthur and Wilson's (1967) island biogeography text. This book was concerned with explaining the equilibrium number of species on islands. It was dealing with the same parameters of colonization and extinction as Levins, but always with colonization from a source area (mainland) to an island. Another real difficulty for the development of the metapopulation concept is that metapopulations function on temporal and spatial scales that are not convenient for ecologists to study; local populations may persist for longer than the life span of the average research grant and metapopulations last longer than that. The growing awareness by ecologists of the role of spatial distributions in population ecology (as seen in each of Chapters 4–6) in the 1980s and early 1990s has undoubtedly hastened the development of the metapopulation concept, though it is worth stressing that there is a difference between a metapopulation and a patchily distributed local population.

#### 7.2.1 Metapopulation models

Levins (1969) distinguished between the dynamics of single populations and a set of local populations. He assumed that individual local populations were either at carrying capacity ( $K$ ) or extinct, thereby ignoring

local dynamics except for colonization and extinction events. The variable  $p_t$  in his model denotes the fraction of habitat patches occupied by a species at time  $t$ . The spatial arrangement of patches is assumed to be of no consequence; individuals in one patch are equally likely to disperse to any of the other patches. The basic Levins model has the following form:

$$dp/dt = \text{colonization rate} - \text{extinction rate.} \quad (7.1)$$

Here,  $dp/dt$  is the rate of change in the fraction of occupied patches and the equation is therefore analogous to population models in which rate of change of abundance is the difference between birth- and death-rates. In his first model, Levins (1969) assumed that the rate of colonization was proportional to  $p$ , the fraction of patches from which potential immigrants were available to colonize empty patches, and to  $1 - p$ , the fraction of unoccupied patches, or targets for colonization. Since all local populations are assumed to be at their carrying-capacity, they all have the same extinction probability and the model becomes:

$$dp/dt = mp(1 - p) - ep, \quad (7.2)$$

where  $m$  is the rate of recolonization of empty patches and  $e$  is the rate of local extinction of patches. Thus the amount of recolonization increases both with the number of empty patches prone to colonization ( $1 - p$ ) and the number of occupied patches able to provide colonizers,  $p$ . Extinctions simply increase with  $p$ . The equilibrium value of  $p$  (obtained by setting  $dp/dt = 0$ ) is:

$$p = 1 - e/m. \quad (7.3)$$

This simple model makes one important point: a metapopulation can only persist if, when small, the rate of establishment of new local populations exceeds the rate of local extinctions. This conclusion, while in itself unremarkable, nevertheless provides us with a means of relating metapopulation dynamics to the structure of the environment, particularly the size and isolation of habitat patches (Hanski, 1989). In addition the model contains the three basic elements necessary for population regulation at the metapopulation level. They are that colonization and extinction events are at least to some extent uncorrelated among local populations, there is dispersal between habitat patches, and

there is some density-dependence in local dynamics (constant  $K$  in the Levins model).

The next level of complexity in single-species metapopulation models comes with the incorporation of local population dynamics into the models. Figure 7.1 shows some examples which suggest that

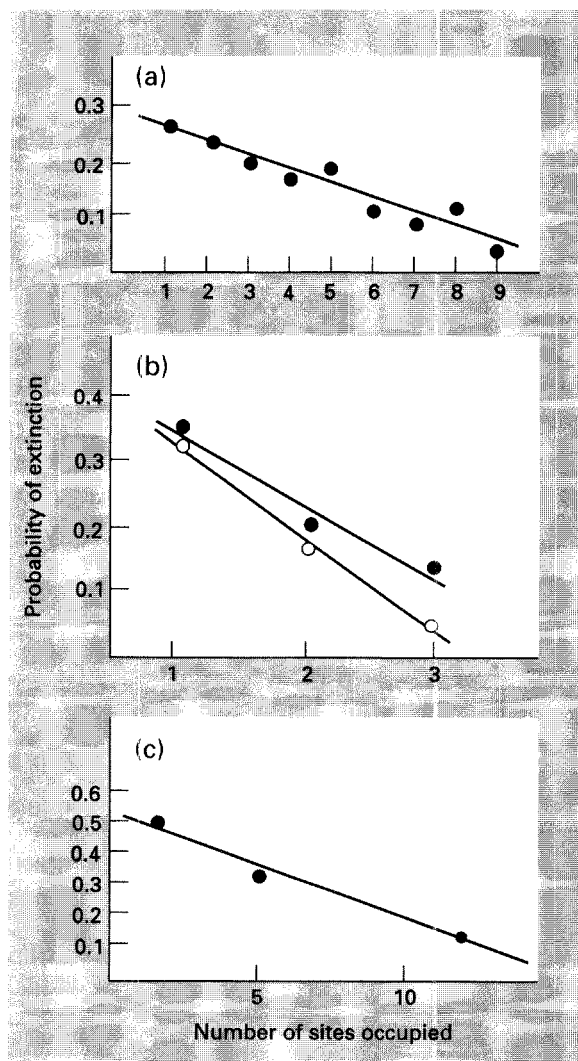


Fig. 7.1 Relationship between the probability of local extinction and  $p$  in (a) mangrove island insects (Simberloff, 1976), (b) leafhoppers (Konthanen, 1950), and (c) freshwater molluscs living in small ponds (Boycott, 1930). (After Hanski, 1991.)

extinction probability is not constant between patches, but decreases as the fraction of patches occupied ( $p$ ) increases. The reasons for this are two well-known phenomena: (i) the increase in extinction probability with declining population size (e.g. Williamson, 1981); and (ii) the observed increase in local population size as  $p$  increases, (e.g. Hanski, 1982; Gaston & Lawton, 1990). This is contrary to the assumptions of the Levins model, which Hanski (1991) then modified accordingly:

$$dp/dt = mp(1-p) - e_0 c^{-ap} p \quad (7.4)$$

where  $e_0$  and  $a$  are two extinction parameters. If  $e_0$  is greater than  $m$ , the model may have two alternative stable equilibria (Fig. 7.2), separated by an unstable equilibrium, a threshold value for metapopulation persistence (Hanski, 1991). The importance of alternative equilibria lies in the possible use of metapopulation models to aid the re-establishment of species in fragmented habitats. If alternative equilibria exist the propagule (or size of the introduction) must be sufficient to push the metapopulation beyond its threshold value.

Further developments in metapopulation models, both single and multi-species, are likely to involve the incorporation of stochastic processes and a closer link between regional and local dynamics (see papers in Gilpin & Hanski, 1991).

### 7.2.2 Examples of metapopulations

In order for species to conform to a metapopulation structure there must be a tendency for local populations to become extinct, and a relatively poor ability to disperse and colonize new habitats. Waterfleas (*Daphnia* spp.) in rockpools (Bengtsson, 1991) and pool frogs in successional ponds (Sjögren, 1991) provide close approximations to the Levins concept. However, some of the most persuasive examples come from studies of butterflies (e.g. Harrison *et al.*, 1988; Thomas & Harrison, 1992).

Thomas and Harrison studied nine metapopulations of the silver-studded blue butterfly *Plebejus argus* in North Wales. This species is patchily distributed wherever it has been studied. It typically occurs in temporary habitats, but despite this, most adults move only short distances. In North Wales, *P. argus* lays its eggs along the margins between bare ground and the vegetation on which the larvae feed, usually on south facing slopes. The larvae are relatively polyphagous (hosts from the Ericaceae, Leguminosae and Cistaceae) and it is oviposition site rather than host plant that limits persistence. The larvae and pupae are also associated with *Lasius* ants, with which it has an extremely close, and probably mutualistic relationship (Jordano & Thomas, 1992). The metapopulations studied by Thomas and Harrison occurred in two main

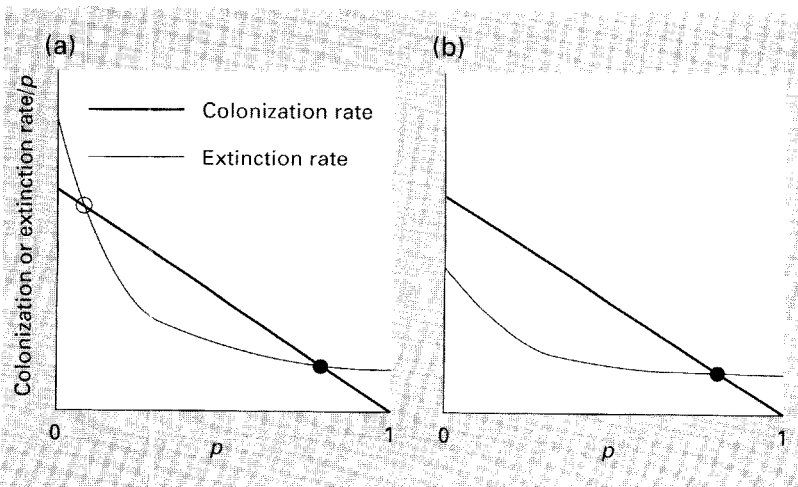
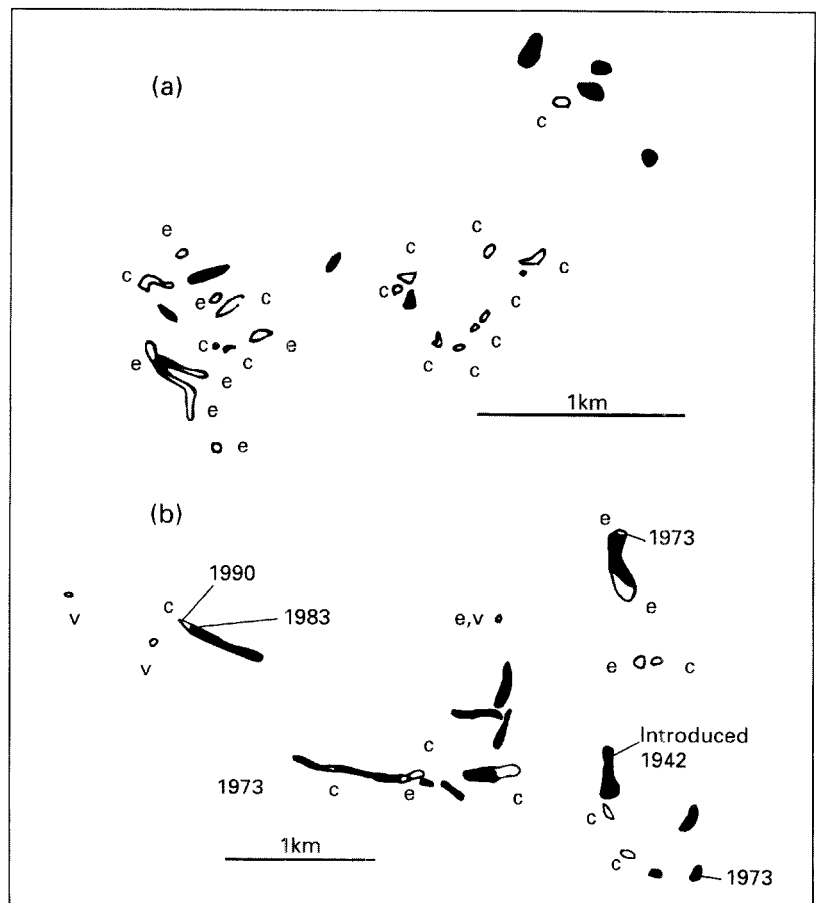


Fig. 7.2 Alternative stable equilibria in a modified Levins model, equation 7.5, which takes into account the empirically observed (Fig. 7.1) negative relationship between extinction probability and  $p$ . The thick line gives the colonization and extinction rates divided by  $p$ . In (b) the two functions have only one intersection point, which is stable, but in (a) there are two intersection points, a stable one (●) and an unstable one (○). In this case the trivial solution ( $p = 0$ ) is also stable. (After Hanski, 1991.)

biotopes, heathland and limestone grassland. In heathland the successional nature of the habitat is maintained by burning, cutting, grazing or disturbance, which all serve to create oviposition sites. In limestone grassland, the suitable microhabitat of vegetation and bare ground can be created and maintained by grazing indefinitely, and succession is extremely slow in any case on similar limestone habitats, such as screes, crags, quarries, etc. Thomas and Harrison (1992) described surveys of suitable sites in North Wales in 1983 and 1990. Examples of the distribution of *Plebejus argus* are shown in Fig. 7.3a and 7.3b for a heathland and a limestone metapopulation. The Dulas Valley limestone metapopulation is of particular interest as it maps the colonization of a network of habitat patches following the introduction in 1942 of 90 females to one patch.

On a regional scale the distribution of *P. argus* was limited by its low dispersal tendency. Suitable habitat only a few kilometres from existing metapopulations remained uninhabited. Evidence that at least some of these habitats are suitable (not just in the minds of human observers) comes from the successful introduction into the Dulas Valley. Within metapopulations local butterfly distribution closely followed that of suitable habitat with most patches within 1 km of existing populations being occupied. As might be expected turnover was greater in heathland, where transient successional habitats remained for relatively short times, than in limestone grassland, where the habitat can be maintained in the suitable successional state for long periods by grazing. In addition heathland habitat patches were generally smaller than those on limestone grassland, and small patches

Fig. 7.3 (a) The distribution of *Plebejus argus* in the South Stacks/Holyhead Mountain heathland metapopulation in 1983 and 1990. Filled outlines indicate areas where *P. argus* was present in both 1983 and 1990. Empty outlines indicate areas where *P. argus* was not present in both time periods: e, presumed extinction (*P. argus* was present in 1983 only); c, presumed colonization (present 1990 only); v, vacant but apparently suitable habitat in 1990. (b) Colonization of the Dulas Valley limestone site by *P. argus*, following the introduction of 90 females in 1942. The 1973 signs give the outermost boundaries of patches occupied in 1971–73. (After Thomas and Harrison, 1992.)



showed higher turnover than large patches in any case.

Whether the individuals in a series of patches should be regarded as a series of separate populations, a metapopulation or as one population with a number of resource patches depends on the distribution of dispersal distances relative to patch size and the distance between patches. If dispersal distances are extremely low relative to the distances between patches, then the patches can be said to hold a series of separate populations. Conversely, dispersal distances are extremely high in relation to distances between patches, then the patches are simply part of the heterogeneity experienced by a single population. The populations of *P. argus* in North Wales described by Thomas and Harrison, particularly those on heathland, are intermediate in these respects and would seem to fit the metapopulation concept reasonably well.

### 7.2.3 Applications of the metapopulation concept

The equilibrium theory of island biogeography proposed by MacArthur and Wilson (1967) is, as we have seen, concerned with the same basic processes as the metapopulation models, namely colonization and extinction. The theory attempted to account for the number of species on real islands or habitat islands, and proposed that the species number was an equilibrium between immigration and extinction rates, themselves determined by island area and distance from the source of colonists. The difference between the MacArthur–Wilson model and the metapopulation models is that in the former there is a mainland which is an inexhaustible source of colonists, and in the latter all colonists must come from existing local populations. The MacArthur–Wilson model is concerned with numbers of species, the metapopulation models are concerned with populations of single species. However, Hanski and Gilpin (1991) and Gotelli (1991) provide a single-species version of the MacArthur–Wilson model analogous to equation 7.1 for changes in the fraction of *islands* occupied:

$$dp/dt = m(1 - p) - ep, \quad (7.5)$$

where  $m$  is now migration from the mainland to the

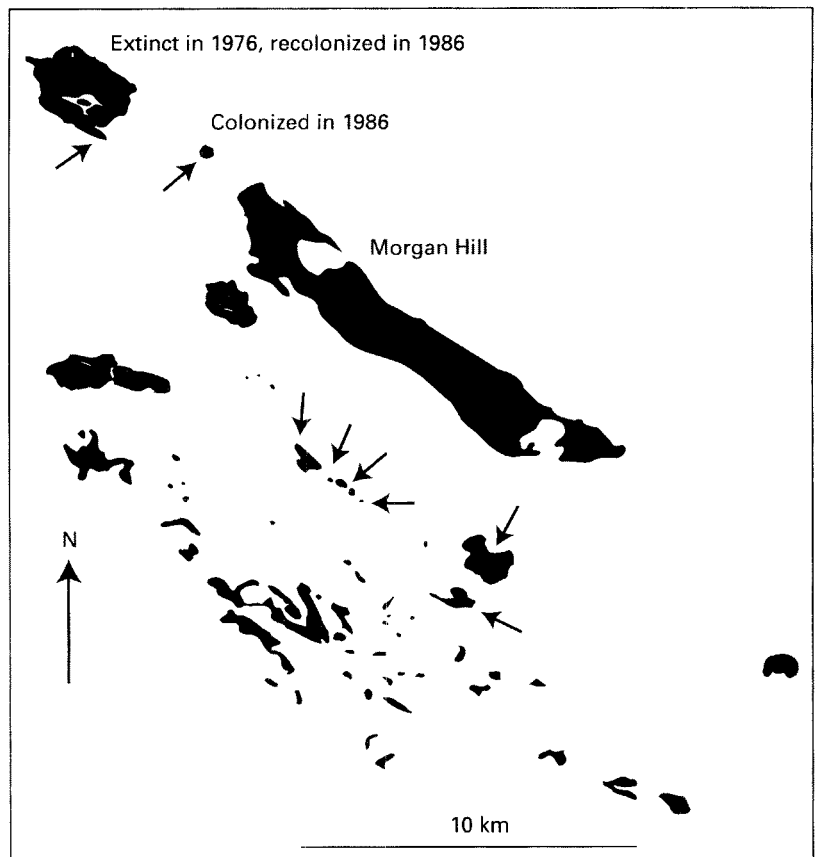
islands. The equilibrium value of  $p$  is:

$$p = m/(m + e), \quad (7.6)$$

which is always positive for islands with any turnover. Equation 7.5 describes the frequency of occurrence of a species when neither immigration nor extinction probabilities are affected by regional occurrences. Most metapopulations probably function somewhere between that described by Levins and the modified MacArthur–Wilson model. It is almost inconceivable that all habitat patches will be so similar that each has the same carrying-capacity, an assumption of the Levins model. Those local populations which are much larger than average will have reduced extinction probabilities and thus function as small mainlands. They may be so large that they are extremely long-lived and the appropriate metapopulation structure is one of an almost permanent patch with transient satellite patches. A good example of such a structure is provided by Harrison *et al.* (1988) for the bay checkerspot butterfly in California (Fig. 7.4). In 1987 the metapopulation consisted of a 2000-ha habitat patch (Morgan Hill) containing of the order of  $10^6$  adult butterflies and nine small populations containing between 10 and 350 adults on patches of between 1 and 250-ha. Of some 27 small habitat patches in the region that were suitable for the butterfly, only those closest to Morgan Hill were occupied. Such a pattern of patch occupancy is not explicable in terms of habitat quality, but it rather reflects the butterfly's limited powers of dispersal. The large population at Morgan Hill acts as the dominant source of colonists to the smaller patches. In this case the persistence of the metapopulation is relatively unaffected by population turnover on the smaller patches.

In the 1970s island biogeography theory was linked with the design of nature reserves (Diamond & May, 1981). How many Amazonian plant and animal species will survive if only 1% of the Amazonian rainforest survives? At what rate will species be lost? Is it best to allocate a certain total area to one large or several small reserves? Species area curves (like Fig. 7.10) offered insights into the first question and the MacArthur–Wilson equilibrium theory held out the promise of a solution to questions like the second

**Fig. 7.4** Metapopulation of the bay checkerspot butterfly *Euphydryas editha bayensis*. The black areas represent patches of the butterfly's serpentine grassland habitat. The 2000-ha patch labelled 'Morgan Hill' supported a population of in the order of  $10^6$  adult butterflies in 1987. The nine smaller patches labelled with arrows supported populations of in the order of between  $10^1$  and  $10^2$  butterflies in that year. Eighteen other small patches were found to be suitable but unoccupied. (After Harrison, 1991.)



and third. As environments become increasingly fragmented, many species, which previously had continuous spatial distributions, may find themselves with a rather more discontinuous one. Species with very poor powers of dispersal in a newly fragmented habitat will simply exist in smaller populations with each one facing an increased probability of extinction. Others with better powers of dispersal are likely to exist as metapopulations. Thus the controversy alluded to above about whether or not an area set aside for nature conservation should be one large or several small reserves (see Simberloff & Abele 1976) is really a metapopulation rather than an island biogeographic problem, particularly when the reserve is being designed for one or a few key species. Metapopulation dynamics provides a natural framework for considering the survival of species in a network of reserves (Hanski, 1989).

Like Hanski (1990) we are tempted to speculate that metapopulation regulation may prove to be as important for many species as traditional population regulation. Tree species in tropical forests have a wide diversity and patchy distributions. There is much less of a tendency in the tropics for species to occur in solid stands than in temperate forests. This means that there can be a considerable nearest-neighbour distance between conspecific trees. Tree canopies of particular species thus effectively become patches of suitable habitat surrounded by a sea of potentially unsuitable (or even downright poisonous) habitat. In the canopies of these trees live a high percentage of the metazoan species on this planet (Erwin & Scott, 1980; May, 1988), many of which are monophagous and oligophagous herbivorous insects. These species may conform to the metapopulation concept, particularly those that have relatively poor dispersal abilities.

This is an exciting scenario for future research and one which cannot, for obvious reasons, be delayed long.

## 7.3 Community structure

### 7.3.1 The role of interspecific competition

Good evidence that interspecific competition can play an important role in determining community structure is provided by an experiment carried out by Putwain and Harper (1970) on a hill grassland site in North Wales that was closely grazed by sheep. The species with which they were most concerned was sorrel, *Rumex acetosella*, which was second in abundance in the community to a grass, sheep's fescue (*Festuca ovina*). *Galium saxatile* (heath bedstraw) was also abundant, and 14 other species of grasses and herbs were present in varying numbers. Specific components of the community were experimentally removed with herbicides by setting up plots of the following types:

- 1 plots sprayed with Dalapon to remove all grasses; this does little and only temporary damage to *Rumex acetosella* and other non-gramineous species (i.e. dicots);
- 2 plots in which individual plants of all dicots except *R. acetosella* were killed by the combined application of the herbicides 2,4-D and Tordon 22K;
- 3 plots sprayed with Paraquat to remove all species except *R. acetosella* which, despite having its above-ground parts scorched, regrows rapidly from buds at the base of the stem; and
- 4 plots in which *R. acetosella* plants alone were killed by spot treatment with Tordon 22K.

There were also control plots that were not sprayed at all.

Spraying took place on 2 June 1965 and then, to distinguish between the effects of treatment on vegetative and seedling growth, seeds were sown in parts of the plots on 20 September 1965. Abundance of *R. acetosella* was monitored throughout the year following treatment, and its dry weight under each regime determined on 5 July 1966. The results are shown in Figs 7.5 and 7.6.

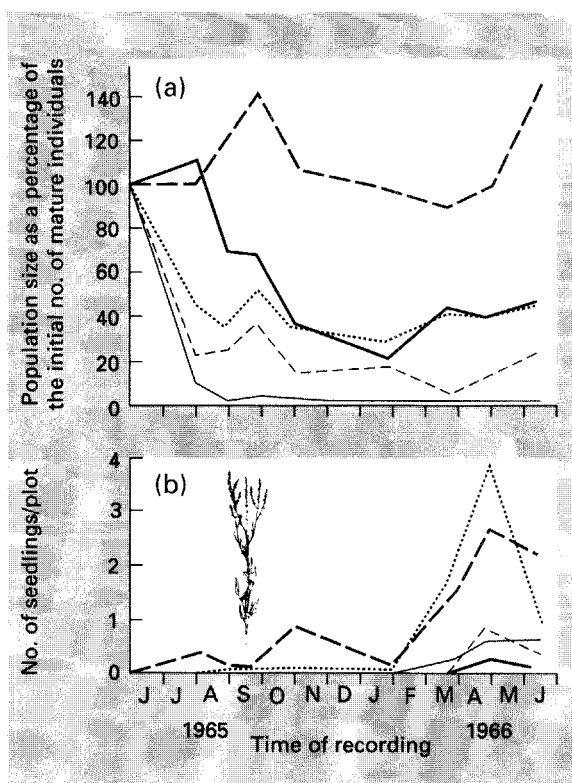


Fig. 7.5 (a) The response of a population of *Rumex acetosella* in a mixed grassland sward to the removal of certain components of the sward, expressed as a percentage of the population in June 1965. (b) Numbers of seedlings per plot. Key to treatments: (—) control; (---) *R. acetosella* removed; (.....) all dicots except *R. acetosella* removed; (- · - · -) grasses removed; (- - - -) all species except *R. acetosella* removed. (After Putwain & Harper, 1970.)

It appears that the growth of mature sorrel plants was unaffected by the removal of dicots, was increased only slightly by the removal of grasses, but was very significantly increased by the removal of both grasses and dicots. The rate of seedling establishment was increased by the removal of grasses, or of dicots, or of the mature plants of *R. acetosella* itself.

The probable explanation is illustrated in Fig. 7.7, which is a diagrammatic representation of *R. acetosella*'s niche relationships within the community. *R. acetosella*, since it exists within the sward, obviously has a realized niche; but it is competitively excluded from a substantial portion of its fundamental niche in

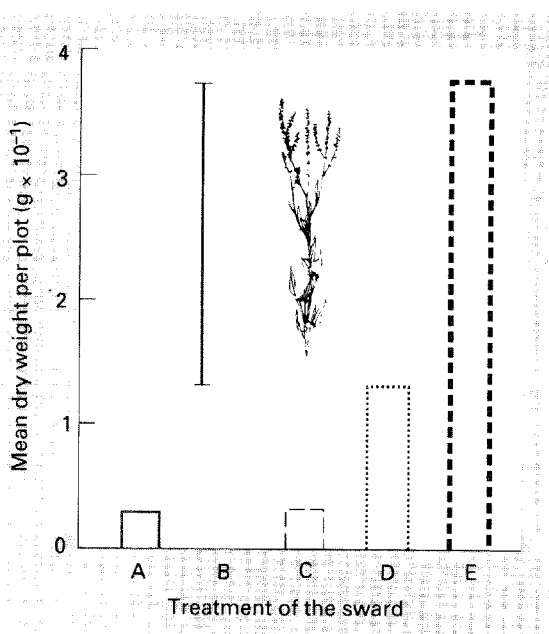


Fig. 7.6 The dry weight (g) of *Rumex acetosella* per plot at the end of the period of observation. For key to sward treatment, see Fig. 7.5. LSD indicated at  $p = 0.05$ . (After Putwain & Harper, 1970.)

this community by the combined action of the dicots, and from a similar but even larger portion by the combined action of the grasses. It is, therefore, only when dicots and grasses are both absent that significant competitive release occurs. It appears, moreover, that the fundamental niche of the sorrel seedlings lies largely within the combined realized niche of the grasses, though other, smaller portions lie within the realized niches of the dicots and the *R. acetosella* adults.

This experiment shows clearly that the distribution and abundance of sorrel is determined to a significant extent by the interspecific competitive interactions occurring within the grassland community. Of course, the precise design of the niches in Fig. 7.7 is quite arbitrary and their important dimensions are not even dimly understood. Nevertheless, the figure does serve to illustrate how communities must often be structured by species being competitively confined to small, realized portions of their fundamental niches.

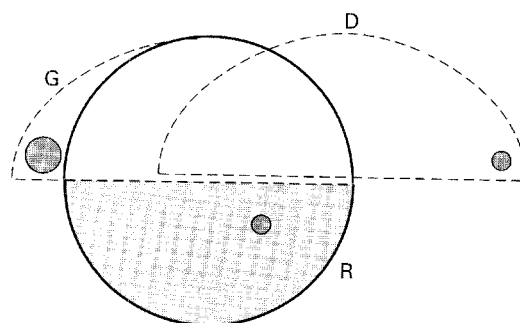


Fig. 7.7 The diagrammatic fundamental niches of *Rumex acetosella* (R), grasses (G) and dicots (D). Light-shaded area: the realized niche of *R. acetosella*; dark-shaded areas: the fundamental niche of *R. acetosella* seedlings. (Modified from Putwain & Harper, 1970.)

We have, remember, seen several similar examples in Chapter 4: seed-eating desert ants showing differentiation in size and foraging strategy; *Panicum* and *Glycine* showing niche differentiation with respect to nitrogen; barnacles partitioning space; bumblebees specializing on flowers of different corolla lengths; plants showing temporal heterogeneity in resource utilization, and so on. In the present context, the importance of these examples is that, in all such cases, the communities are structured, and species diversity increased, by resource partitioning based on competitive exclusion.

### 7.3.2 The role of predation

The most famous piece of evidence supporting the importance of predators in determining community structure is provided by the work of Paine (1966), and their role is succinctly stated (as a hypothesis) by Paine himself: 'Local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species'. Paine presented some correlational support for this hypothesis, but his most persuasive evidence was experimental.

On the rocky shores of the Pacific coast of North America the community is dominated by a remarkably constant association of mussels, barnacles and one starfish; and Fig. 7.8 illustrates the trophic rela-

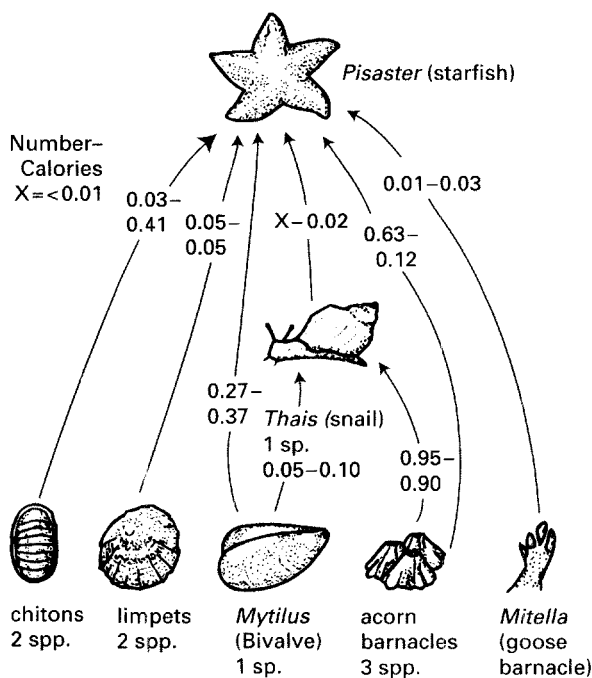


Fig. 7.8 The feeding relationships by numbers and calories of the *Pisaster* dominated subweb at Mukkaw Bay. The specific composition of each predators diet is given as a pair of proportions: numbers on the left, calories on the right. (After Paine, 1966.) 1 calorie (non-SI unit) = 4.186 joules.

tionships of this portion of the community as observed by Paine at Mukkaw Bay, Washington. The data are presented both as the numbers and as the total calories consumed by the two carnivorous species in the subweb: the starfish *Pisaster ochraceus* and a whelk *Thais emarginata*. Apparently this food web is based on a barnacle economy, with both major predators consuming them in quantity. Note, however, that in terms of calories the barnacles are only about one-third as important to *Pisaster* as either *Mytilus californianus*, a bivalve, or the browsing chiton *Katherina tunicata*.

For several years from June 1963, Paine excluded all *Pisaster* from a 'typical' piece of shoreline at Mukkaw Bay about 8 m long and 2 m in vertical extent. An adjacent control area was left unaltered; and line transects across both areas were taken irregularly, and the number and density of resident macroinvertebrate and benthic algal species mea-

sured. The appearance of the control area did not alter. Adult *Mytilus californianus*, *Balanus cariosus* (an acorn barnacle) and *Mitella polymerus* (a goose-necked barnacle) formed a conspicuous band in the mid-intertidal; while at lower levels the diversity increased abruptly, with immature individuals of the above species, *Balanus glandula* in scattered clumps, a few anemones of one species, two chiton species (browsers), two abundant limpets (browsers), four macroscopic benthic algae (*Porphyra*, *Endocladia*, *Rhodomela* and *Corallina*), and the sponge *Haliclona* (often browsed upon by *Anisodoris*, a nudibranch) all present.

Where the *Pisaster* were excluded, however, the situation changed markedly. *Balanus glandula* settled successfully throughout much of the area, and by September 1963 it had occupied 60–80% of the available space. By the following June, however, the *Balanus* themselves were being crowded out by small, rapidly growing *Mytilus* and *Mitella*; and this process of successive replacement by more efficient occupiers of space continued, leading eventually to an experimental area dominated by *Mytilus*, its epifauna, and scattered clumps of adult *Mitella*. The benthic algae, with the exception of *Porphyra*, tended to disappear due to a lack of space, while the chitons and larger limpets tended to emigrate because of an absence of space and a lack of appropriate food.

Interpretation of Paine's experiment must be tempered by the admission that the altered system may not have reached an equilibrium (Paine, 1966). Nevertheless, it is clear that the removal of *Pisaster* led to a marked decrease in diversity, despite an actual increase in the size of the standing crop. There was a change from a 15-species system to a trophically simpler eight-species system, and of the species that disappeared, some were and some were not in the normal diet of *Pisaster*. It seems, then, that the influence of *Pisaster* on the community is at least partly indirect; by eating masses of barnacles and the competitively dominant *Mytilus*, and thus keeping space open, *Pisaster* enhances the ability of other species to inhabit the area. When space is available, other organisms, for instance chitons, settle or move in, and form major portions of *Pisaster*'s nutrition. Thus, in the absence of predation there is an increased

**Table 7.1** Effects of density on seed mortality amongst tropical trees. All published observations and experiments known from tropical forests are included (After Connell, 1979)

Location	Vegetation type	Plant species	% Mortality		References
			Dense	Sparse	
Queensland, Australia	Evergreen rainforest	<i>Cryptocarya corrugata</i>	100	99	Connell, 1971
Costa Rica	Deciduous forest	<i>Acacia farnesiana</i>	79.7	79.6	Janzen, 1975
Costa Rica	Deciduous forest	<i>Scheelea rostrata</i>	35.7	6.1	Wilson & Jansen, 1972

tendency for competition at lower trophic levels to go to completion, driving species to extinction; but by its presence, *Pisaster* keeps many of these populations well below their carrying-capacity. Competitive exclusion is, therefore, commonly avoided, and the diversity of the community enhanced. In short, it seems that, in the present case at least, Paine's hypothesis is correct: predation prevents competitive exclusion and, therefore, increases community diversity.

In theory, predation can have an even more potent effect on species diversity when it is frequency-dependent, i.e. when there is predator switching leading to a 'type 3' functional response (section 5.7.4). Prey species will then be disproportionately affected when they are common, and this should lead to a large number of rare prey species. Unfortunately, in practice, there is little positive evidence that this occurs (Connell, 1979). Nevertheless, by examining all the available data on seed and seedling mortality in tropical trees, Connell (1979) was able to show that, in many cases, there is decreased survivorship (i) when density is high (Table 7.1), and (ii) in the immediate presence of established adults (Table 7.2). Conversely, these tables also show that there were several other cases when this was not so. Overall, while it is clear that such frequency-dependent predation does occur in nature (leading, no doubt to increased diversity), it is equally clear that its occurrence is by no means the general rule.

### 7.3.3 The role of disturbance

Following Connell (1979), we shall take 'disturbance' to be the indiscriminate, catastrophic removal of all

individuals from an area. As such it may take a wide variety of forms: e.g. lightning, storms, land-slips or even indiscriminate predation. In general terms, its effect will be to prevent communities from reaching an equilibrium; parts of them, at least, will be repeatedly returned to early, colonizing stages of succession. Its more specific effect on species diversity, however, will depend on the nature of the equilibrium community itself; and this, in turn, will depend on the various processes—competition, predation and so on—also discussed in this chapter. Nevertheless, a plausible, general relationship between disturbance and diversity has been proposed by Connell (1979)—the 'intermediate disturbance hypothesis'—and the role of disturbance in determining community structure can be usefully discussed in this context.

Connell recognized, essentially, three levels of disturbance (Fig. 7.9a). Where disturbances are frequent and large, the community will tend to be dominated by opportunistic, fast-colonizing species, with, perhaps, a few individuals of intermediate, secondarily colonizing species, probably present as juveniles. Such a community will have a simple structure and a low diversity (left-hand side of Fig. 7.9a). At the other extreme, where disturbances are rare and small, the diversity will depend on the importance of what Connell calls 'compensatory mechanisms', i.e. predation, resource partitioning, and so on. As we have seen, where these are prevalent diversity will be high. In their absence, however, only highly competitive, late-succession species will be able to survive, and diversity will be low (right-hand side of Fig. 7.9a). Conversely, at intermediate levels of disturbance, even in the absence of compensatory mechanisms, there

**Table 7.2** Survivorship of seeds or seedlings either near or far from adult trees of the same species. All known published field experiments or observations in tropical forests are listed, but in some cases typical, rather than total, results are presented. (After Connell, 1979.)

Location	Vegetation type	Plant	Fitness parameter		Near adult	Far from adult	References
Queensland, Australia	Evergreen rainforest	<i>Cryptocarya corrugata</i>	% seed mortality		99.8	99.5	Connell, 1971
Queensland, Australia	Evergreen rainforest	<i>Eugenia brachyandra</i>	% germination in first year		14.8	14.0	Connell, 1979
Queensland, Australia	Evergreen rainforest	<i>Planchonella</i> sp.	% seedling mortality in trenched plots		68	21	Connell, 1971
Puerto Rico	Evergreen rainforest	<i>Euterpe globosa</i>	% non-viable seeds	1970 1971	95–100 0–11	83–100 0–20	Janzen, 1972a
Costa Rica	Deciduous forest	<i>Scheelea rostrata</i>	% seed mortality		33.8	35.7	Wilson & Janzen, 1972
Costa Rica	Deciduous forest	<i>Sterculia apetala</i>	Number of herbivorous bugs per seed		5.2	1.8	Janzen, 1972b
Costa Rica	Deciduous forest	<i>Spondias mombin</i>	% seed mortality		50	45	Janzen, 1975
Costa Rica	Deciduous forest	<i>Dioclea megacarpa</i>	% shoot tips eaten		86.4	16.7	Janzen, 1971

will probably be a few adults of fast-colonizing species, many individuals of mid-succession, secondarily colonizing species, and even some individuals, possibly juveniles, of late-succession species. Overall, therefore, diversity will be high (centre of Fig. 7.9a); in the comparative absence of compensatory mechanisms, the species diversity of communities will be highest at intermediate levels of disturbance.

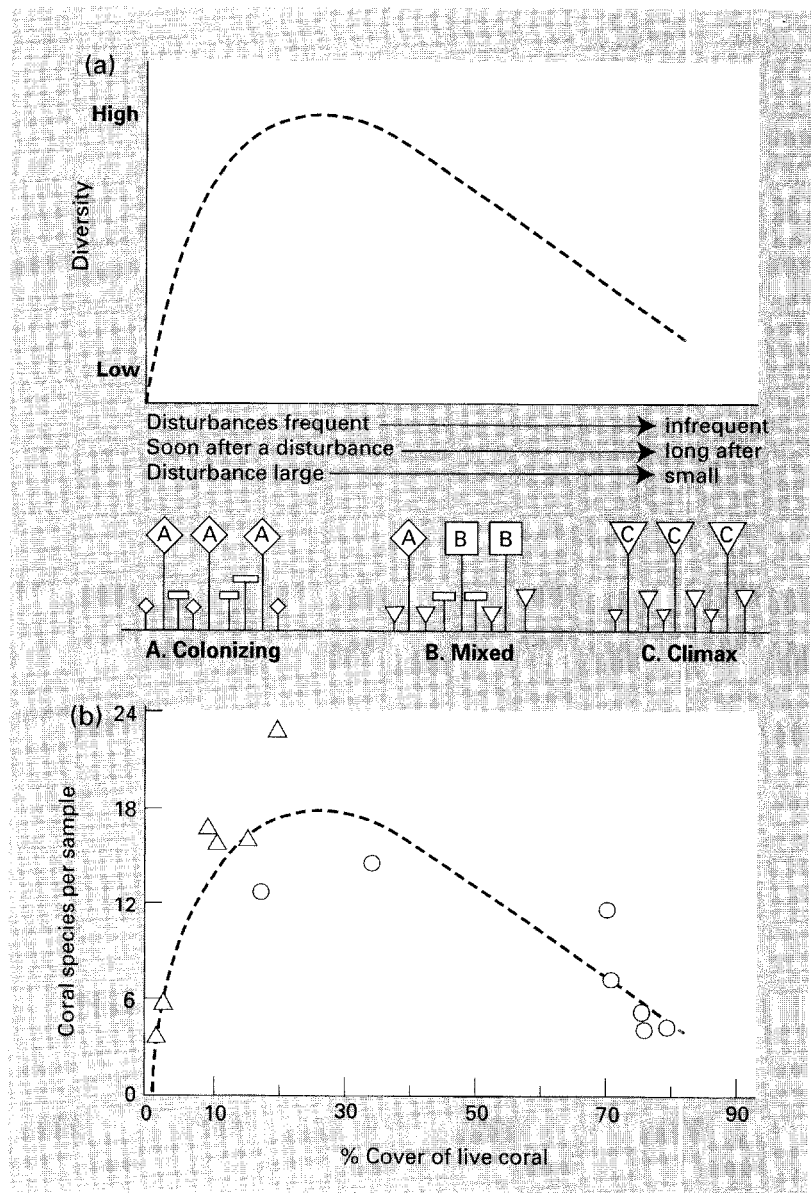
Some of Connell's evidence in support of this hypothesis is shown in Fig. 7.9b, where the data come from observations on a coral reef off the coast of Queensland, Australia. Disturbance, resulting either from hurricane damage or from the effects of anchoring boats on the reef, is measured as the percentage of a site that is devoid of any live coral, and it is indeed apparent that diversity (number of species per sample) is highest at intermediate levels of disturbance. As further evidence, Connell points out that even in tropical rainforests, which we tend to think of as

exhibiting very high diversity, areas that are largely undisturbed (like the Bindongo forest in Uganda) come to be dominated by a single species of tree (in this case, ironwood).

Overall, therefore, we can accept that, in some cases, diversity will be highest at intermediate levels of disturbance; and that generally, large frequent disturbances will tend to decrease diversity. Conversely, the effects of disturbance on diversity will be much less clear-cut whenever compensatory mechanisms are sufficiently potent to ensure that stable climax communities exhibit a high degree of diversity themselves.

#### 7.3.4 The role of instability

All populations are, to a greater or lesser extent, liable to become extinct; and whenever this occurs, the structure of the community containing that population will obviously change. However, this liability is



**Fig. 7.9** (a) Connell's 'intermediate disturbance' hypothesis, involving (A) opportunistic species, (B) secondarily colonizing species, and (C) climax species. (b) Data in support of the hypothesis from Heron Island, Queensland from damaged ( $\Delta$ ) and undamaged ( $\circ$ ) sites. (After Connell, 1979.)

bound to be greater in some communities than others, and in this sense some communities must be more unstable than others. Yet the communities with structures conferring stability are the ones most likely to be observed, because they persist. Structural instability must, therefore, be an important determinant of observed community structure.

The search for what, inherently, leads to instability

has been the province of theoretical ecologists, and, to paraphrase May (1979), two intertwined conclusions have emerged.

1 In 'randomly constructed' model ecosystems, an increase in the number of species in a community is associated with an increased dynamical fragility and a diminished ability to withstand a given level of environmental disturbance. Thus, relatively stable or

predictable environments may permit fragile, species-rich communities to exist; while relatively unstable or unpredictable environments will support only a dynamically robust, and therefore relatively simple, ecosystem.

2 Real ecosystems are not assembled randomly. They are the products of long-running evolutionary processes. We are therefore bound to ask: what special structural features of real ecosystems may help to reconcile community complexity with dynamical stability? In other words, since instability will tend to simplify communities, what observable features of community structure can be deemed to exist by virtue of the stability they confer on complex, species-rich systems? The proposed 'role of instability' will then be the 'selection' of these features.

Attempting to discover what these features might be has also been the province of theoretical ecologists; and, as yet, these attempts have been largely speculative. Nevertheless, there are several interesting possibilities (May, 1979). May (1972), for instance, and Goh (1978) have suggested (from the analysis of models) that ecosystems will be more robust if they consist of 'loosely coupled subsystems'. This term describes a situation in which a community consists of several parts ('subsystems'), *within* which there is considerable biological interaction, but *between* which there is very little interaction. This, according to Lawton and Pimm (1978) and Beddington and Lawton (1978), is at least consistent with the observation that most insect herbivores are monophagous or oligophagous, giving rise to relatively discrete food chains even in species-rich plant communities. However, empirical evidence generally fails to give positive support to the hypothesis (Pimm & Lawton, 1980).

Another feature of natural communities possibly subject to selection by instability is the length of food chains, which rarely consist of more than four or five trophic levels. The conventional explanation for this is that length is limited by the inefficiency of energy flow from one trophic level to the next (there is insufficient energy left to support the higher trophic levels). Yet, as Pimm and Lawton (1977) have pointed out, this cannot, by itself, explain why food chains are about as long in the tropics (where energy input is high) as they

are in the barren Arctic (where energy input is low). An alternative explanation, however, was provided by Pimm and Lawton themselves. By studying the stability properties of various Lotka–Volterra models, they argued that long food chains may typically result in population fluctuations that are too severe for top predators to exist. In other words, only relatively short food chains are sufficiently stable to be observed in natural communities.

Finally, Pimm and Lawton (1978) have explored the relationship between omnivory and stability by studying model ecosystems based on Lotka–Volterra equations. Broadly speaking, they conclude that omnivory and overall dynamical stability are easier to reconcile if the omnivores and their prey are of similar size and population density, a situation that most commonly pertains to insect parasitoids. As May (1978b, 1979) suggested, this may account for the diversity of insects in general and the diversity of parasitoids in particular.

Overall, then, while its precise role remains largely the subject of theoretical speculation, it is quite clear that instability can play a crucial part in determining the structure of natural communities.

### 7.3.5 The role of habitat size and diversity

As Gorman (1979) has pointed out, Great Britain has 44 species of indigenous terrestrial mammals, extant or recently extinct, but Ireland, just 20 miles farther into the Atlantic, has only 22; and while this might conceivably reflect the difficulties the mammals have in crossing water, it actually affects bats as much as any other group: only seven of Britain's 13 species breed in Ireland. Furthermore, of Britain's 171 species of breeding birds, only 126 are recorded as breeding in Ireland, and 24 of these do so only occasionally. For example, there are no woodpeckers in Ireland (though there are plenty of trees), no little or tawny owls, and no marsh or willow tits.

The most likely explanation is that Great Britain is far larger than Ireland. But size can exert its effects in two quite separate ways. Perhaps the most obvious explanation is that differences in habitat size are important because large habitats are more diverse.

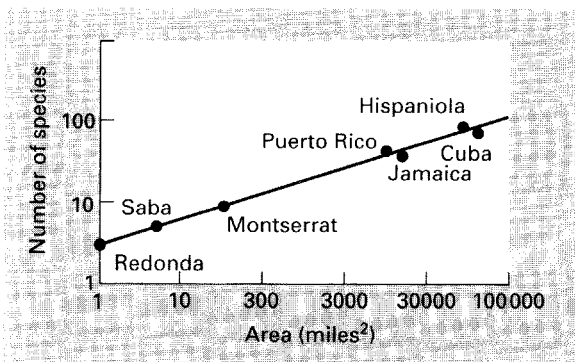


Fig. 7.10 The number of amphibian and reptile species living on oceanic West Indian islands of various sizes. (After MacArthur & Wilson, 1967.)

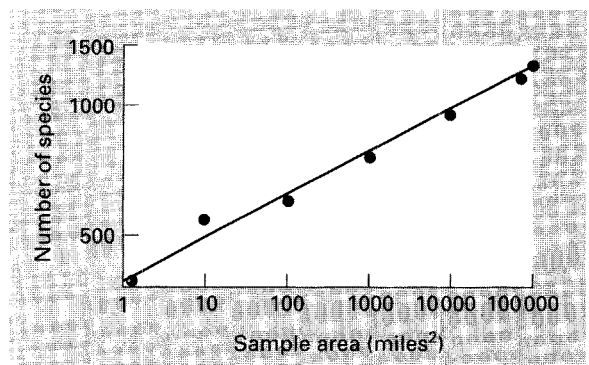


Fig. 7.11 The species area curve for the number of flowering plants found in sample areas of England (Williams, 1964). (After Gorman, 1979.)

But there is a second explanation that applies whenever habitats can be thought of as islands (either real islands, or 'habitat islands' of one type surrounded by a 'sea' of another habitat type). Larger islands support larger populations that have a relatively low probability of becoming extinct. In addition, larger islands represent a larger 'target' for colonization by species not already present (MacArthur & Wilson, 1967). On two counts, therefore, extinction and immigration, we can expect larger islands (i.e. larger habitats) to support more species. Note, too, that this is an explanation for the fact that (small) islands generally support fewer species than a nearby (larger) mainland.

A typical relationship between the number of species living on an island and the island's area is illustrated in Fig. 7.10, for the amphibians and reptiles living on oceanic islands in the West Indies (MacArthur & Wilson, 1967). The logarithm of species number rises with the logarithm of island area in a remarkably linear fashion, and the slope (0.30) is very much in line with those obtained in other examples. For organisms ranging from birds to ants to land plants, in both real and habitat islands, the slopes of such log-log plots mostly fall within the range 0.24–0.34 (Gorman, 1979). The role of island (i.e. habitat) size as a determinant of species number (and thus community structure) is therefore, well established.

An indication of the fact that size acts through two

mechanisms, however, is provided by data in Fig. 7.11 (Williams, 1964). This, too, is a plot of log species number against log habitat size, but size in this case pertains to arbitrary sampling areas within a mainland. Once again, on this log-log plot, the number of flowering plants rises linearly with the size of sampling areas in England. But the slope—around 0.1—is noticeably lower than those from the island examples, and falls near the range typical for mainland studies: 0.12–0.17 (MacArthur & Wilson, 1967). The crucial point is that habitat size can only act via habitat diversity in such cases. These arbitrary areas are continually exchanging organisms with surrounding areas, and they are not, therefore, subject to the considerations of extinction and colonization that apply to isolated islands. Thus, mainland slopes from 0.12 to 0.17 reflect the effects of habitat diversity, while the increased slopes on islands react the additional size effects peculiar to island biogeography.

Overall we can see that an increase in habitat size will lead to an increase in species number, and thus to an increase in the complexity of community structure. This may result from the indirect effects of habitat diversity, or from effects peculiar to the island nature of many habitats; and while it is often difficult to partition the total effect into these two components, there is no doubt that both are of very widespread importance.

### 7.3.6 Conclusions

We have seen that a variety of factors *can* influence community structure. Yet, in truth, it has to be admitted that precise statements as to their relative potencies must await further advances in our knowledge and understanding. Nevertheless, certain tentative conclusions can be drawn.

Perhaps the most significant of these is that a good case can be made for the *constancy, predictability and productivity of the abiotic environment* being of absolutely crucial importance in determining community structure. This conclusion stems from a number of considerations.

1 In general terms, diverse, basically fragile ecosystems appear to be relatively stable in constant, predictable environments (section 7.3.4).

2 More specifically, niches can be stably packed more tightly in predictably productive environments (section 4.15). This suggests that interspecific competition will be most potent as a mechanism promoting diversity under such circumstances (section 7.3.1).

3 Equally specifically, the stable existence of top predators will be favoured in predictably productive environments (Paine, 1966). It is, therefore, in such cases that they will be most potent in keeping potential competitors below their carrying-capacities, and thus promoting diversity still further (section 7.3.2).

4 Finally, these other mechanisms will tend to reinforce one another. High diversity at a lower trophic level will certainly provide for niche diversification (and thus increased diversity) at the next highest trophic level; and it is possible that this will lead to an increased intensity of predation, and thus a further increase in diversity, at the lower trophic level. Small 'inherent' differences in community structure are, therefore, likely to become exaggerated. Note, however, that this reinforcement will occur whatever the

cause of the inherent differences. Note, too, as another aspect of this reinforcement, that those effects of habitat size that are attributable to habitat diversity (section 7.3.5) will themselves be influenced by increases in the diversity of the biotic aspects of a habitat.

In short, there is good reason to believe that the constancies, predictabilities and productivities of abiotic environments are crucial, underlying determinants of community structure: and that competition, predation and ecosystem instability are *mechanisms* through which they exert their influence. This is almost certainly the explanation for the single most important cline of increasing diversity: from the poles to the tropics.

This view is opposed, to some extent, by Connell's 'intermediate disturbance hypothesis' (section 7.3.3), since a constant, predictable environment is likely to be one with a low level of disturbance. Conversely, Connell's 'disturbance' requires the indiscriminate removal of species from an area, and an environment can be inconstant and unpredictable without this happening. It is, therefore, possible that this hypothesized mechanism acts independently of the other factors considered, and influences diversity in a wide range of environments. Finally, the 'island' effects of habitat size (section 7.3.5) are likely to superimpose their influences on community structure wherever they occur; and, to the extent that all environments are patchy, they are likely to occur everywhere.

To summarize, then, we know a reasonable amount about the potentialities of the various factors determining community structure, but rather less about their actual potencies and the patterns of their action in nature. Discovering the rules through which communities are constructed from populations is one of the many exciting challenges that confronts population ecology today.